

# **Why do some species feed on others: comparative advantage of predation over competition by MERA**

Jade, Mar 12

Predation as one of the most common species interactions emerged early in the evolutionary history. However, how it originated at the first place is not clear. The question is, why is feeding on another species more advantageous than simply competing with it for the fundamental resource, when predation requires a lot of energy and there is a limited efficiency ( $\approx 10\%$ , according to Lindeman's Ten Percent law) in transferring energy between trophic levels? Meanwhile, the body size relationship between a predator and its prey is not a straightforward one. The prey is usually smaller than the predator (mice vs cats, insects vs birds), however, though not as common, small species could prey on larger ones (hyenas on wildebeests). There is no universal explanation for these various patterns.

Here with MERA, I am going to show the conditions for predation to be more advantageous than competition (and the converse), from which a first explanation for why predation and competition both exist within a community emerges. The various body size relationship between the

predator and the prey can also be explained. In the end, multi-species ( $> 2$ ) scenarios will be discussed, with the body size - abundance relationship compared among different scenarios (competition, larger species prey on smaller species, smaller species prey on larger species).

## 1 Competition vs Predation: two-species scenario

Suppose we have two species, each with resource requirement  $\theta_i (i = 1, 2)$  and relative individual distinguishability  $D_{r,i}$ . While the resource available in each step is a constant, the species can both consume the resource directly and therefore become competitors, or one of the species become the predator and feed on the other species for energy. In the following I will separately derive the steady state for each case, then compare them to get the conditions for which scenario is more desirable for the potential predator species.

### 1.1 Competition

First let's consider the case where the two species are competing with each other for the resource. From the analytical solution to steady state of MERA we have:

$$\hat{N}_i = \frac{2}{e} (C\theta_i)^{\frac{1}{D_{r,i}-1}} \quad (1)$$

where  $\hat{N}_i$  is the abundance of species  $i$  at steady state.  $C$  is a constant for all species

$$C = 2e^{\lambda-1} \quad (2)$$

$e$  is the base of the natural logarithm.  $C$  can be calculated from substituting Eq. 1 into the resource constraint:

$$R = \theta_1 \hat{N}_1 + \theta_2 \hat{N}_2 \quad (3)$$

## 1.2 Predation

Then we consider a second case where species 2 feeds on species 1. Since species 1 has no competitors for resource any more, the dynamics of it is simply described by

$$\theta_1(N_1 + G_1) = R \quad (4)$$

$G_1$  is the net number of individuals added to species 1 after one allocation period, or the net growth rate. In the write-up “Justifications for addition assumptions of MERA predator-prey interaction” on Dec 15, I have clarified that the number of prey individuals the predator consumes in each step must be the net growth rate of the prey at steady state, which is annotated by  $\hat{G}_1$ , and  $\theta_1(\hat{N}_1 + \hat{G}_1) = R$ . Meanwhile, species 2 is the only predator feeding on species 1 and therefore at steady state

$$\theta_2 \hat{N}_2 = \theta_1 \hat{G}_1 \quad (5)$$

Notice that on the right hand side of the equation  $\hat{G}_1$  is multiplied by  $\theta_1$ , since on the left hand side  $\theta_2$  is still in the unit of the fundamental resource. In other words, if it is to be counted in the unit of individuals of species 1,  $\theta_{2,species1} = \theta_2/\theta_1$ , or equivalently how many individuals of species 1 could suffice to feed an individual of species 2.

In Eq. 5 we have assumed no energy is lost in transferring energy from the prey to the predator. If we consider the efficiency to transfer energy from the prey to the predator is  $\tau$  ( $< 1$ ), then Eq. 5 has to be rewritten as:

$$\theta_2 \hat{N}_2 = \tau \theta_1 \hat{G}_1 \quad (6)$$

Substituting into Eq. 4 we get the resource constraint:

$$R = \theta_1(\hat{N}_1 + \hat{G}_1) = \theta_1(\hat{N}_1 + \frac{\theta_2 \hat{N}_2}{\tau \theta_1}) = \theta_1 \hat{N}_1 + \frac{\theta_2}{\tau} \hat{N}_2 \quad (7)$$

Notice that this is different from the resource constraint when the two species compete with each other (Eq. 3).

Applying the second additional assumption introduced in the Dec. 15 write-up - the predator deliberately choose the optimal level of predation so that its abundance is the highest at steady state given the resource constraint - the dependence of the predator abundance on the resource at steady state can be determined simply by:

$$\hat{N}_2 = \frac{\tau R}{2\theta_2} \quad (8)$$

Eq. 8 is obtained by setting  $G_1$  to its biggest possible value:

$G_1 = N_1 = R/2\theta_1$ , corresponding to optimal predation as is illustrated in the above.

Now we have the steady state abundance for species 2 as a competitor (Eq. 1) and predator (Eq. 8), we can compare them to reveal when one is more advantageous than the other.

### 1.3 Comparative advantage space for competition and predation

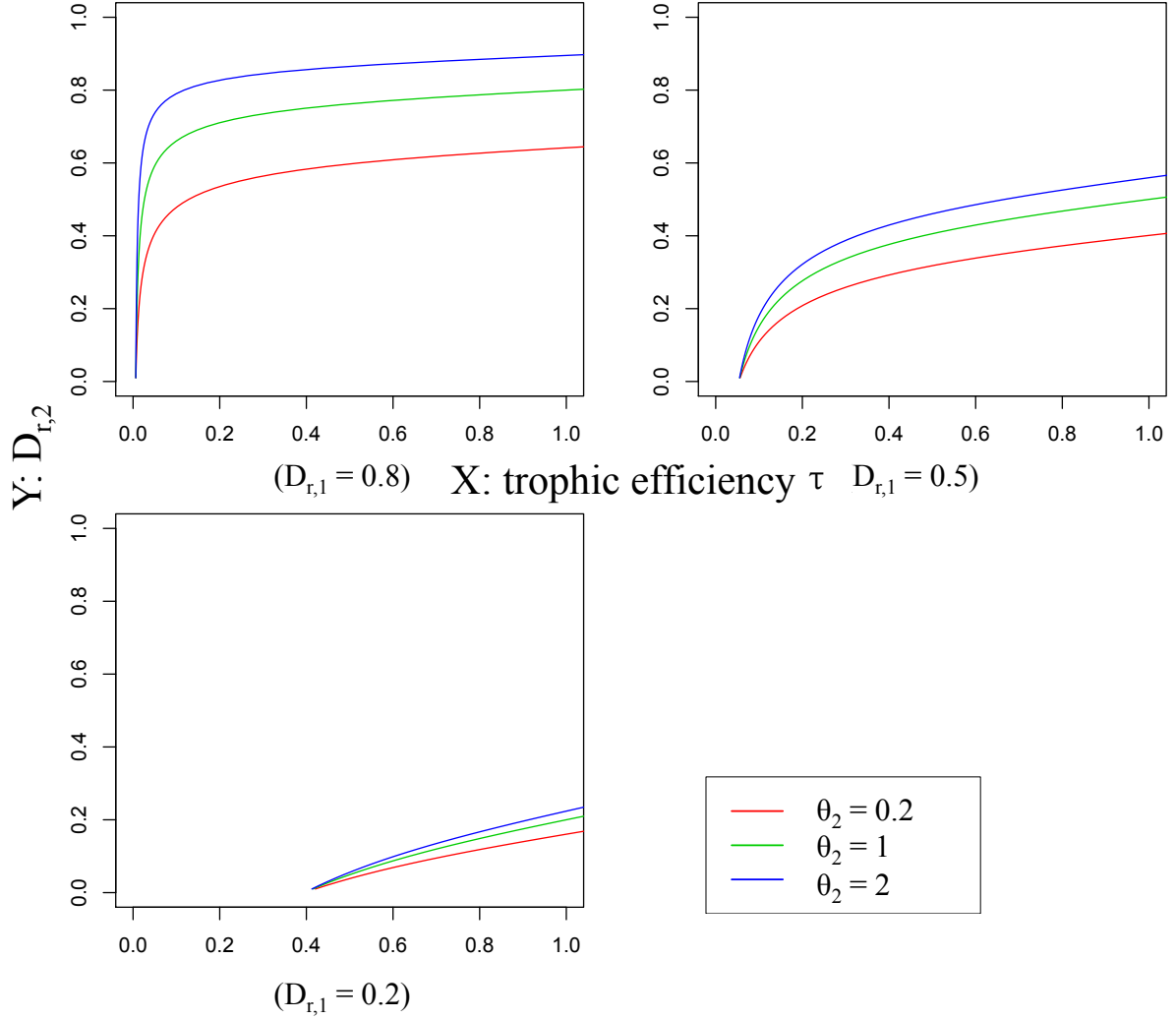
In all of the following analysis  $\theta_1 = 1, R = 1000$ . The condition for the steady state abundance of species 2 as a competitor and a predator to be the same is given by equating Eq. 1 and Eq. 8:

$$\frac{2}{e}(C\theta_2)^{\frac{1}{D_{r,2}-1}} = \frac{\tau R}{2\theta_2} \quad (9)$$

This corresponds to the case where competition and predation are equally advantageous (in terms of steady state abundance) for species 2. Notice that when  $D_{r,1} = D_{r,2} = 0$ , Eq. 1 reduces to  $\hat{N}_i = \frac{R}{2\theta_i}$ , the case where the energetic equivalence rule (EER) holds and each of the two species gets half of the total resource. In this case, however, Eq. 9 can never be met with  $\tau < 1$ . In other words, **when conspecific individuals are perfectly indistinguishable for both species, it is always more advantageous for a species to become a competitor instead of a predator of the other species.**

The more general cases are shown in the following graph, where Eq. 9 is

plotted on a  $D_{r,2}$  vs  $\tau$  scale. I will call this curve the “indifference curve”, since on it the species is equally well off as a competitor or as a predator.



Notice that on the left (upward) side of the indifference curve, it is more advantageous for species 2 to be a competitor (left side of Eq. 9 is bigger than the right side) and therefore could be named as the “**competition advantage space**”, while on the right (downward) side of the curve being a predator is more beneficial and therefore could be named as the

“predation advantage space”.

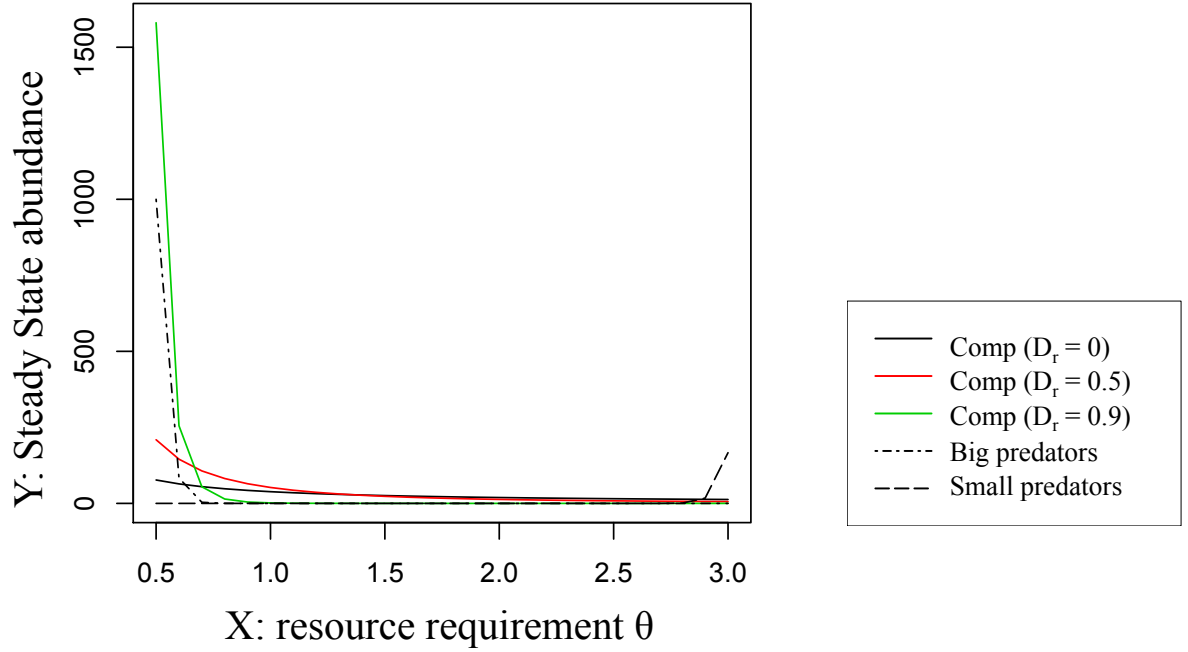
From the graph we can see that the bigger the  $D_{r,2}$  and the smaller the  $\tau$ , the more advantageous it is for species 2 to be a competitor compared to being a predator and vice versa. Meanwhile, the bigger the resource requirement of species 2 ( $\theta_2$ ) is, the larger the predation advantage space is compared to the competition advantage space as is shown by the curves of different colors. Assuming resource requirement  $\theta$  is positively correlated to the body size of the species, this means that **all else equal, it is more advantageous for a bigger species to become a predator. But it is still possible for a smaller species to become a predator** (indicated by the space under the red curve in each graph).

Looking across the graphs we can also see that the bigger the relative individual distinguishability of species 1 ( $D_{r,1}$ ), the larger the predation advantage space is compared to the competition advantage space. This means that **when the individuals of the other species are highly distinguishable** (possibly associated with high intraspecific variation, clear metapopulation structure, etc.), **it is more advantageous for the species to be a predator instead of a competitor.**

## 2 Abundance - body size relationship: multi-species scenarios

Now that the condition for comparative advantage of predation vs competition has been revealed under the two-species scenario, next I will show in a multi-species ( $> 2$ ) scenario how the abundance-body size relationship changes when the species interact in different manners. To start with, here we only explore three simplest scenarios where 1) all species are in competition with each other, 2) the species form a food chain (one species at each trophic level) where a species always feed on the next (in body size) smaller species and is prey to the next bigger species, 3) same as 2) except that the predator-prey body size relationship is reversed (a species always feed on the next bigger species and is prey to the next smaller species). Also for simplicity, I assume the species all have the same  $D_r$ .





Directly applying Eq. 1 for the first scenario where all species are competitors (item 1 - 3 in the legend), the higher the  $D_r$ , the steeper the abundance decay is from the smallest to the largest species. Notice that the first item in the legend indicates the energetic equivalence rule (EER) when  $\theta$  is interpreted as the metabolic rate.

The multi-species predation scenarios are calculated by repetitively applying Eqs. 4 - 8 at each trophic level and therefore the steady state abundance of the species  $i$  (also at the  $i_{th}$  trophic level from the bottom

prey) is given by

$$\begin{aligned}\hat{N}_i &= \frac{R}{\theta_i} \times \left(\frac{\tau}{2}\right)^{i-1} && (\text{if } i > 1) \\ &= \frac{R}{2\theta_i} && (\text{if } i = 1)\end{aligned}\tag{10}$$

For the first predation scenario where bigger species prey on smaller species (item 4 in the legend), we can see that the abundance decay is very steep, which means that **it is fast increasingly unlikely for species to become higher level predators**, even if they are bigger. For the scenario where smaller species prey on bigger species (item 5 in the legend), the trend of the abundance-body size relationship is reversed (abundance increasing with body size). The predicted steady state abundances shown on the curve suggest that this trophic structure where **smaller species feeding on bigger species is disadvantageous for all species except for the biggest one**.

The pattern is of course largely influenced by the assumption of a perfectly linear food chain structure (only one species at each trophic level) and therefore could only provide preliminary inference. More complex scenarios for a food web structure will be explored in the future.

### 3 Summary

In this write-up, only the steady states are examined. The dynamics are particularly uninteresting in all of these scenarios since there is only one

species at each trophic level and the constraint of complete resource exploitation makes the allocation process trivial (as is shown in Eq. 4, any deviation from the steady state will be eliminated with one step). In future work, more species will be included in each trophic level and then the dynamic dependence and temporal trajectories could be studied.

In the fundamental cases explored in this write-up, just examining the steady state patterns leads to interesting inferences. For details please refer to the bolded text in the above sections. To roughly summarize, the MERA framework provides a preliminary yet straightforward and parsimonious explanation for what drives a species to be a predator instead of a competitor and why the predator tends to be bigger than the prey: individual distinguishability  $D_r$ , resource requirement  $\theta$  are both influencing factors. The patterns from the multi-species scenarios suggest that, for the energetic equivalence rule (EER) to hold, not only conspecific individuals have to be indistinguishable ( $D_r = 0$ ), all species have to be on the same trophic level. Either violated, EER cannot be observed.